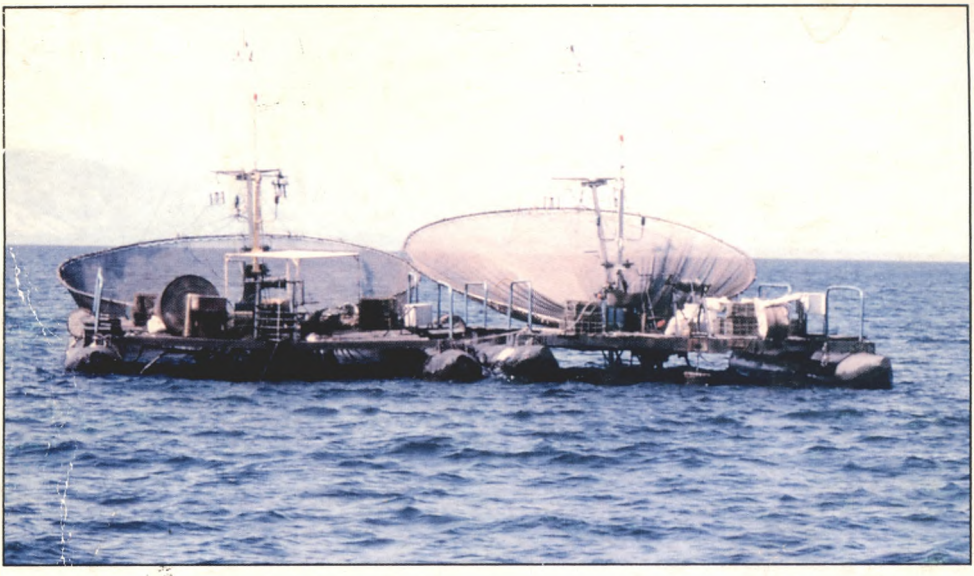

ADVANCES IN THE ECOLOGY OF LAKE KARIBA

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Cover Top:	Typical ringnets as utilized in Kapenta fisheries on Lake Kariba
Bottom:	Lake Kariba: The littoral area and draw-down zone
Back cover:	Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

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A REVIEW OF ZOOPLANKTON ECOLOGY IN LAKE KARIBA

Brian E. Marshall

INTRODUCTION

The zooplankton of Lake Kariba has attracted attention from a number of workers in the years since the lake was created. Like every other group, it provides an opportunity to study the evolution of a lacustrine community from a riverine one. It is strongly influenced by the seasonal cycle in the lake, as well as by the inflowing rivers, which allows us to learn something about nutrient dynamics and the processes of production in the lake. The zooplankton was greatly altered by the introduction of the sardine, *L.miodon*, from Lake Tanganyika and this unplanned experiment has contributed to our understanding of the effect of planktivorous fish on zooplankton communities. Finally, an understanding of the zooplankton became even more necessary following the development of flourishing fishery for *L. miodon* which made it the most important fish species in the lake.

This work is briefly reviewed in this paper. It considers firstly, the species composition in the lake and then describes the changes brought about by the sardine. A discussion of the seasonal and diurnal cycles is followed by a consideration of the importance of the inflowing rivers. A central theme of this review is the relationship between the zooplankton and its major predator, *L. miodon*.

SPECIES COMPOSITION

Very little was known about zooplankton in the Zambezi River before the Kariba Dam was built. Some specimens were collected in April 1956 but their densities were very low as the river was in flood (Jackson 1961). They included some species that later became abundant in the lake, amongst them *Diaphanosoma excisum* and *Mesocyclops* identified in Jackson (1961), and elsewhere in the literature, as *M. leuckarti*, which is now known not to occur there).

All organisms increased in abundance once the lake was created (Balinsky and James 1960) and 62 species have now been recorded in the zooplankton (see Green, 1985, for a full list drawn from various sources). They include one medusa, *Limnocnida tanganyicae*, 40 rotifers and 3 species of the dipteran *Chaoborus* (*C. anomalus*, *C. ceratopogones* and *C. edulis*). The remaining species are crustaceans and include 9 copepods: 3 calanoids (*Tropodiaptomus* and *Thermodiaptomus* spp.) and 6 cyclopoids, the most important of which is *Mesocyclops ogunnus*, frequently referred to as *Mesocyclops leuckarti* in the

literature. Nine species of *Cladocera* have been recorded with *Diaphanosoma excisum* and *Bosmina longirostris* generally being the most abundant of them.

A species of shrimp, *Limnocaradina tanganicae*, was apparently introduced along with the sardines from Lake Tanganyika in 1967–68 (Bell-Cross and Bell-Cross, 1971). This was done on the grounds that pelagic shrimps were important food items for the sardines in Lake Tanganyika (Matthes 1965–66). Nothing is known about the fate of these crustaceans.

Lake Kariba is similar in many respects to Lake Albert, being about the same size with a large river inflow and comparable fish species, i.e. without the explosive radiation of cichlid fishes found in other large African lakes (Green 1985). It has a greater diversity of rotifers although Lake Kariba has a rather more diverse crustacean fauna (Table 4.1). It is unlikely that all nine species of planktonic cladocera still exist in Lake Kariba and Green collected only five in 1983. Rotifers and crustacea were less diverse in Lake Turkana which may be a consequence of that lake's high salinity (Green 1985).

Table 4.1 A comparison of the number of species in the main groups of zooplankton in some African lakes and reservoirs. Abbreviations and sources are as follows: Kb = Kariba, Ab = Albert, Tk = Turkana, Kj = Kainji (Green 1985); Cl = Cleveland, Ch = Chivero (Elenbaas and Grundel 1994); Md = the total number in 8 small (0.9–43.5 ha) reservoirs in the Marondera area, Zimbabwe, Ny = the total number in 10 small ones (6.6–40.6 ha) in the Nyanga area, Zimbabwe (Green 1990).

	Kb	*Ab*	*Tk*	*Kj*	*Cl*	*Ch*	*Md*	*Ny*
Rotifera	40	62	10	58	19	17	20	19
(excluding *Lecane*)	30	40	9	52	18	16	20	16
Cladocera	9	5	5	7	8	8	7	7
Copepoda	9	7	7	7	6	5	9	3

The diversity of both pelagic rotifers and crustacea was greater in Lake Kariba than it was in Lake Chivero and the Cleveland Dam near Harare and in a number of reservoirs in the Marondera and Nyanga districts of Zimbabwe (Table 4.1). In the case of the rotifers, at least, this is probably a consequence of its larger size since Green (1990) showed that there was a general relationship between area and rotifer diversity in African lakes.

Prior to the introduction of *Limnothrissa miodon*, the zooplankton of Lake Kariba was similar in many respects to that of other man-made lakes in Zimbabwe (Table 4.2). The most important crustacea tended to be the larger cladocerans, notably *Daphnia* and *Ceriodaphnia*. Amongst the copepods, the larger diaptomids were generally rather more abundant than the cyclopoids. Rotifers made up 44% and 49% (by numbers) of the total zooplankton in Lake Chivero and the Cleveland dam, respectively (Elenbaas and Grundel 1994) but they were apparently much less important in Lake Kariba (Bowmaker 1973). This may, of course, be a sampling artefact since different sampling methods were used.

Table 4.2 The relative abundance (% by numbers) of crustacean zooplankton in Lake Kariba in 1967–68, i.e. prior to the establishment of *Limnothrissa*, and in some Zimbabwean reservoirs. The values for Marondera and Nyanga are the means for 8 and 10 small dams respectively. Data from Bowmaker (1973), Elenbaas and Grundel (1994) and Green (1990)

	Kariba	*Chivero*	*Cleveland*	*Marondera*	*Nyanga*
Diaphanosoma	2.1	2.5	3.9	0.5	1.4
Daphnia	0.8	6.3	13.2	62.2	47.5
Ceriodaphnia	69.1	11.5	0.4	7.5	1.0
Bosmina	7.3	9.7	1.3	3.5	3.0
Others				0.2	1.2
Diaptomids	15.0	48.0	56.2	2.2	17.6
Cyclopoids	4.9	22.0	25.0	13.7	29.0

THE IMPACT OF PREDATION

The introduction of *Limnothrissa miodon* in 1967–68 was to bring about far-reaching changes in the ecology of the lake (Marshall 1991). The zooplankton community was especially affected. Prior to this introduction it was dominated by large cladocerans, such as *Ceriodaphnia* and *Diaphanosoma* and by calanoid copepods (diaptomids). The larvae of *Chaoborus*, which are partly benthic, were the major predators although the jellyfish *Limnocnida tanganyicae* may also have been significant predators when their medusae were abundant, e.g. in the early seventies (Mills 1973). Small cladocera, nauplii and rotifers were relatively unimportant (Figure 4.1).

There is no evidence to suggest that the jellyfish has been affected by the sardines. It is still abundant in the lake from time to time sporadically appearing in large numbers and sardines appear to avoid areas where the medusae are abundant (unpublished observations). According to Dumont (1994), medusae can be protected by their nematocysts and also by transparency, reducing visibility to predators. The medusae take refuge in deep waters during daylight, perhaps to avoid light as well as predators.

In contrast, *Chaoborus* was soon affected since it appears to be especially vulnerable to predation by fishes (Lynch 1979). In 1967–68 there was an average of 362 larvae m^{-2} in the benthos of the Mwenda estuary (Bowmaker 1973) but their density had decreased by half to 192 m^{-2} by 1970 (Mitchell 1975). Although many *Chaoborus* may be carried into the lake as part of the invertebrate drift of the inflowing rivers (Mills 1976) it may now be extinct in the lake itself. There have been no reports of this species in recent samples and adults have not been collected around the lake shore (Marshall 1991).

The other planktonic organisms were also markedly affected. Larger crustaceans, notably the diaptomids, *Ceriodaphnia* and other daphniids, declined rapidly, becoming scarce by 1970 and virtually absent by 1972 (Table 4.3). The diaptomids were largely replaced by smaller cyclopoids and the large cladocera by *Bosmina*. The rotifers moved from being an almost negligible group to one that was numerically the most important.

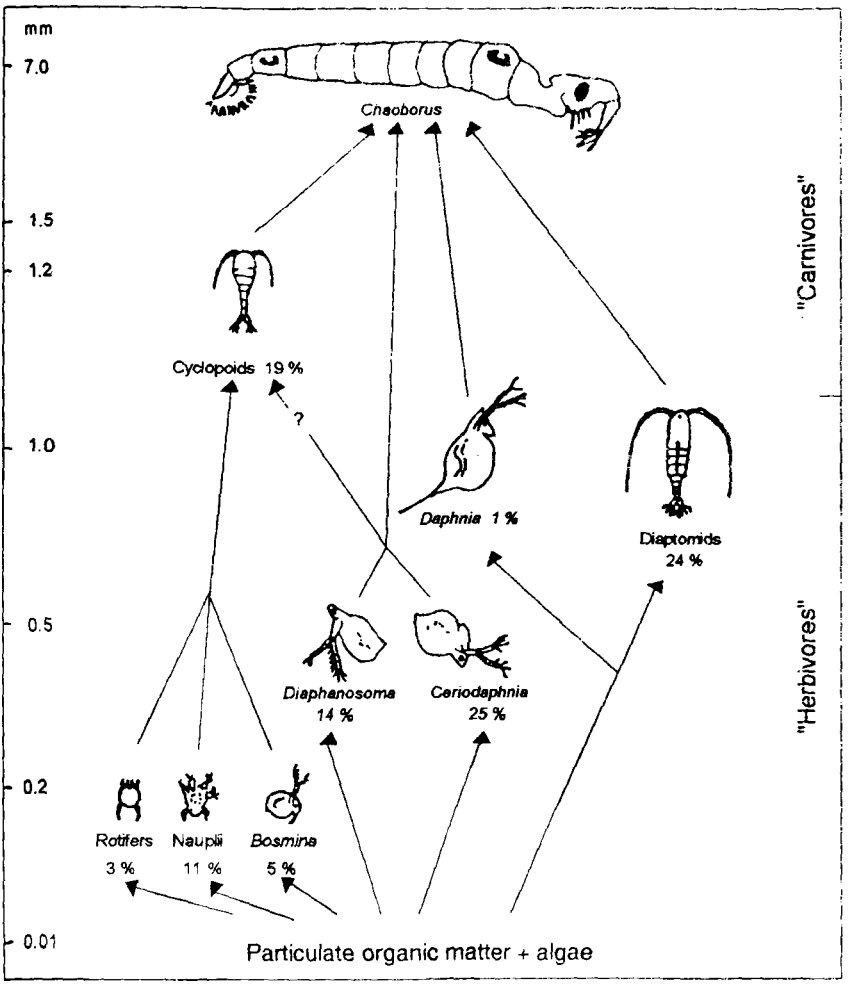

Figure 4.1. The structure of the zooplankton community in 1967–68, at the time the sardines were introduced but before they had become established. The abundance of each group is given as % dry weight. Redrawn from Bowmaker (1973).

The larger cladocera now only survive in areas where they are protected from the sardines. Thus, zooplankton were much more abundant in Crocodile Creek, a shallow inlet off the Mwenda estuary than they were in the estuary itself or in the main lake (Table 4.4). The proportion of crustacea also increased as the water became shallower so that they were more numerous than rotifers at the shallowest stations. Although the sardines breed in the littoral zone, the fry move into deeper water as they grow and the adult fish are seldom found in very shallow water (Cochrane 1978). The native fish species, which live in this area, feed on zooplankton to some extent but it is not an important component of their diet (Mitchell 1976) and they are unlikely to have a major impact.

Table 4.3 Changes in the relative abundance of the major groups of zooplankton in Lake Kariba, 1967–1983. The values are means of the available data and are expressed as percentages of relative abundance (no m^{-3}). The symbol + denotes values of less than 0.1%. Data from Bowmaker (1973), Mitchell (1975), Begg (1976), Cochrane (1978) and Green (1985)

	1967–68	*1970*	*1972*	*1975–76*	*1983*
Diaptomids	14.3	0.2	0	+	0
Cyclopoids	4.7	12.5	10.1	13.8	1.1
Nauplii	11.1	16.4	17.1	3.1	14.8
Bosmina	7.4	15.9	17.1	10.5	2.8
Ceriodaphnia	69.3	14.3	0	0.3	0
Diaphanosoma	2.2	0.2	0	+	0
Daphniids	0.9	0.2	0	0	0
Rotifers	+	40.3	55.7	72.3	81.3

Table 4.4 The abundance (no l^{-1}) of zooplankton in the open waters of Lake Kariba, in the Mwenda Estuary and in Crocodile Creek, a shallow inlet leading off the estuary, August 1983 (from Green 1985). The values are means with percentages given in brackets; the symbol + denotes values of less than 0.1. Haul depth refers to the depth over which the sample was taken

Area	*Lake Kariba*		*Mwenda Estuary*		*Mwenda Estuary*		*Crocodile Creek*		*Crocodile Creek*	
Station N	*1–6*		*1–5*		*6–10*		*1–6*		*7–9*	
Haul depth (m)	10		10		4.8		0.2		0.03	
Diaptomids	·		·		0.2	(0.3)	3.7	(2.2)	518.8	(8.9)
Cyclopoids	0.1	(1.1)	0.7	(3.1)	0.5	(0.8)	0.6	(0.4)	122.2	(2.1)
Daphnia	·		0.1	(+)					53.1	(0.9)
Moina	·		·		0.2	(0.3)	1.0	(0.6)	34.2	(0.6)
Diaphanosoma	·				0.1	(0.2)	1.8	(1.1)	243.3	(4.2)
Ceriodaphnia	·				·					
Bosmina	0.2	(2.3)	0.1	(0.4)	10.1	(15.4)	18.9	(11.5)	2495.6	(42.7)
Nauplii	1.3	(14.9)	1.4	(6.1)	4.5	(6.8)	23.9	(14.5)	1706.7	(29.3)
Keratella	5.2	(59.9)	15.2	(66.8)	33.3	(50.4)	76.4	(46.4)	471.1	(8.1)
Other rotifers	1.8	(20.7)	5.3	(23.3)	17.2	(25.6)	38.4	(23.3)	187.8	(3.2)
Crustacea	1.7	(19.5)	2.3	(10.1)	15.7	(23.7)	50.0	(30.3)	5173.9	(88.7)
Rotifers	7.0	(80.5)	20.5	(89.9)	50.5	(76.3)	114.8	(69.7)	658.9	(11.3)

Another consequence of predation was a significant decrease in the biomass of the zooplankton. In 1967–68 the mean biomass in the Mwenda estuary was 228 mg m^{-3} (dry weight) (Bowmaker 1973), whilst it was only 2.26 mg m^{-3} in Sanyati Basin in the late seventies (Magadza 1980) and 15.75 mg m^{-3} in 1985–87 (calculated from data in Masundire 1994). The differences between the last two values may simply reflect variability in the zooplankton population which fluctuates from year to year (Table 4.5). The causes of these variations remain uncertain but may be linked to the size of the sardine population or to the availability of nutrients.

Table 4.5 The mean abundance (no l^{-1}) of cladocera and copepods in the Sanyati basin, Lake Kariba in 1975–76 and 1985–86. Data from Cochrane (1978), Marshall (1980) and Masundire (1989a)

	1975–76	*1979*	*1985–86*
Cladocera	15.3	2.03	3.63
Copepods (adults)	1.63	2.15	0.97
Copepods (nauplii)	3.60	1.68	3.89

Predation may also have induced morphological changes in some species. Andersson and Stenson (1989) noted that the body length of *Bosmina* was about 25% and 33% greater in samples from the mouths of the Nyaodza and Bumi rivers respectively and that *Bosmina* were uniformly large in the western Mlibizi Basin. They also noted that the spines on the rotifer *Brachionus falcatus* were considerably longer in specimens from open water compared to those from the rivers. This was attributed to the increased turbidity in the river mouths and the western basin (although no data were given) which afforded the crustaceans a measure of protection from the sardines. They noted, however, that this could also be a consequence of nutrient enrichment in these areas. This is highly probable since the zooplankton in Lake Kariba show clear responses to nutrient availability, as will be seen later.

THE SEASONAL CYCLE

Together with the thermal cycle in the open waters of Lake Kariba, the hydrological cycle in the rivers controls the abundance of the zooplankton and will be summarized briefly here:

- The lake is stratified from about August until May when overturn takes place and it becomes isothermal (see introduction this volume). The nutrients that are retained in the hypolimnion during the stratification period are released at overturn and become available to organisms in the upper layers.
- Although the nutrient dynamics of the lake have not been studied in detail, it is evident that the quantities available are regulated by the inflowing rivers (Lindmark, this volume). These rivers are highly seasonal, flowing from about November to April and the flood waters tend to flow into the deeper waters (Bowmaker 1976) thus carrying much of their nutrient load into the hypolimnion. The extent of the flood determines the quantity of nutrients released at overturn which occurs shortly after the rivers have ceased to flow strongly. Thus poor rainy seasons are likely to cause a decrease in the productivity and biomass of various pelagic communities; this relationship has already been established for the sardines (Marshall 1982, 1988).

These factors produce a distinctive cycle of abundance in the zooplankton, first noted by Bowmaker (1973) and described in more detail by Begg (1974). In 1971, the lake was stratified from January until the end of May with the thermocline being present at about 20 m depth (Figure 4.2a).

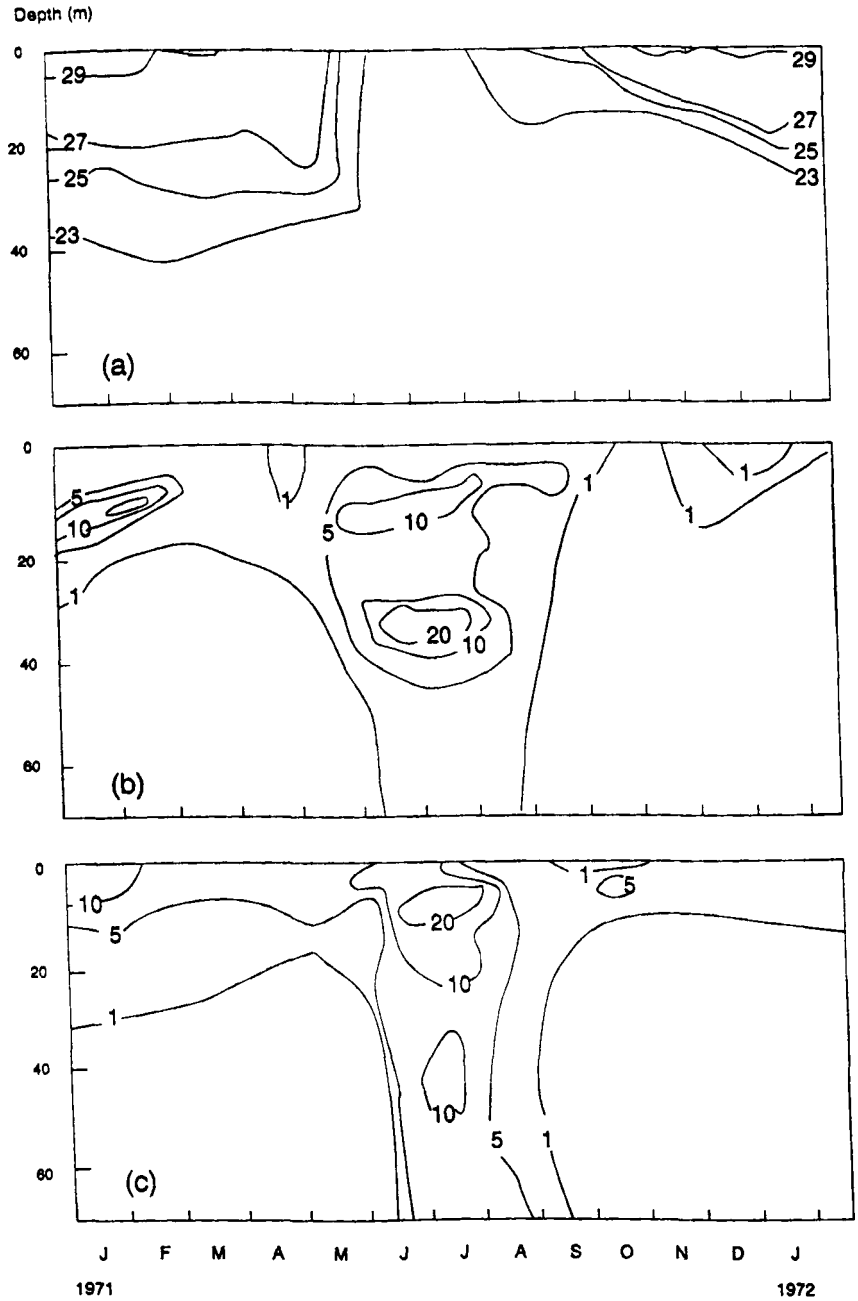

Figure 4.2 The relationship between the abundance of some elements of the zooplankton and the thermal cycle in Lake Kariba, January 1971 to January 1972, (from Begg 1974). (a) water temperatures (°C) in relation to depth (greatly simplified); (b) the abundance (no l^{-1}) of *Bosmina longirostris* in relation to depth; (c) the abundance (no l^{-1}) of *Keratella tropica* in relation to depth. *Mesocyclops* has not been included owing to uncertainties in the original figure

The density of the zooplankton was relatively high at first but it declined from the end of March as the river flows decreased. Very little zooplankton was recorded below 20 m because of the low levels of oxygen in the hypolimnion. Overturn occurred at the end of May and the nutrients released from the hypolimnion caused an immediate increase in zooplankton abundance (Figures 4.2b and c). The animals were also able to extend their distribution when oxygen was present in the deeper waters. Stratification began again in September; the thermocline was initially present at about 5 m but it moved to 20 m by December. The numbers of zooplankton decreased rapidly and had not recovered by the end of January 1972. This was because of the severe drought of 1972–73 when the lake gained no water from direct rainfall or the secondary rivers, compared to an input of 10.20 km^3 in 1971–72 (Zambezi River Authority, personal communication). The effect of this drought was also noted in the Mwenda estuary where plankton numbers declined during 1973 (Mills 1977).

The influence of river flow and the thermal cycle was further demonstrated by Marshall (1988a) who investigated the relationships between phytoplankton, zooplankton and sardines in relation to river flow and the thermal cycle. Both the phytoplankton and the zooplankton followed the cycle closely, with a major peak in abundance in July, following overturn, and a smaller one during the rainy season when the rivers were flowing (Figure 4.3). *Limnothrissa* followed it less closely since its numbers were low during the rainy season, when breeding takes place (Cochrane 1978) and its numbers reached a peak in August one month later than the plankton.

The influence of predation in the seasonal cycle is presently unknown but recent work on *Bosmina* indicates the complex relations that exist between nutrient supply and predation (Figure 4.4). In 1986, the biomass of *Bosmina* was relatively low until overturn, which began at the end of May, when it increased sharply. At the same time, individual animals grew larger and their mean length rose from around 0.27 mm to 0.30 mm. These increases were presumably a response to the increased food supply that followed the release of nutrients from the hypolimnion at overturn. During this time, predation pressure was very high because the transparency of the water had increased and so had the biomass of the sardines.

Indeed, the close relationship between the changes in the mean length of *Bosmina* and the relative abundance of the sardines is striking. It suggests that the growth of individual *Bosmina* is regulated by food availability rather than the intensity of predation. This runs counter to the ideas of Andersson and Stenson (1989) although they did comment on the possible importance of food.

The relationship between the biomass of *Bosmina* and that of the sardines is rather different. A small, early peak of abundance of both species occurred in March but the main increase in *Bosmina* biomass was in June and July when the abundance of sardines was still very low. Sardine abundance reached a peak in August and this may have caused the sharp decline in the *Bosmina* biomass that took place then. The sardines decreased in September whilst *Bosmina* increased again, perhaps because of the decline in predator numbers. Their individual size was decreasing, however, which suggests that a lack of food was beginning to affect them. This could have come about because the lake was beginning to stratify again in September locking up nutrients in the hypolimnion.

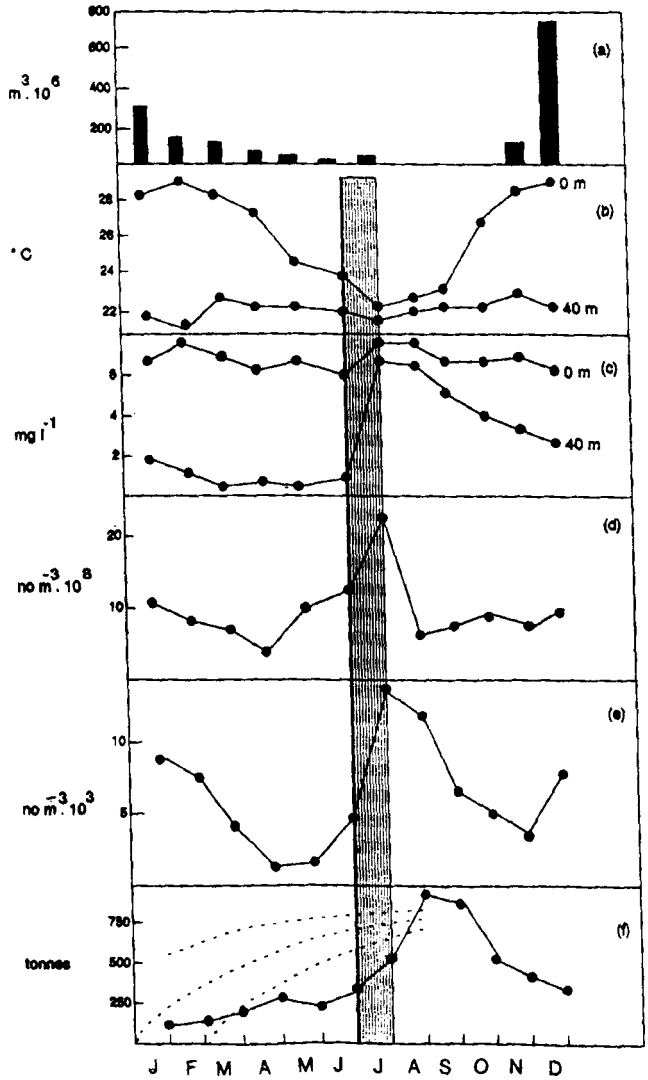

Figure 4.3 The relationships between physico-chemical variables and the abundance of plankton and sardines in the Sanyati basin, Lake Kariba, in 1979; (a) flow of the Sanyati and Nyaodza Rivers (km^2); (b) water temperature (°C) at the surface and at 40 m depth; (c) the concentration of dissolved oxygen ($mg\ l^{-1}$) at the surface and at 40 m depth; (d) phytoplankton abundance ($no\ l^{-1}$); (e) zooplankton abundance ($no\ l^{-1}$); (f) the monthly sardine catch (t), the broken lines indicate the growth of fish (mm) spawned in September, December and February. The vertically hatched column denotes the period of overturn. From Marshall (1988a)

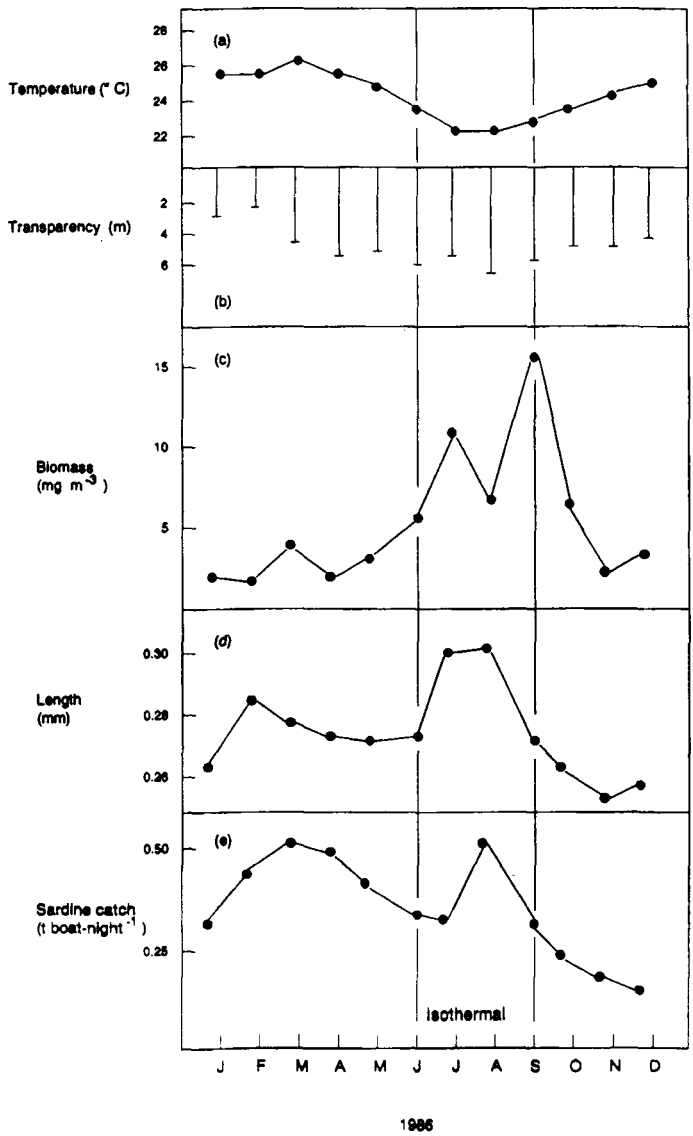

Figure 4.4 The relationship between the mean length and biomass of *Bosmina longirostris* and the mean temperature, transparency and relative abundance of *Limnothrissa miodon* in the Sanyati basin, 1986: (a) surface temperature (°C), from Masundire (1992); (b) transparency, measured as Secchi disc visibility (m), from Masundire (1991b); (c) biomass of *B. longirostris* (mg m^{-3}, dry weight), from Masundire (1994); (d) the mean length of *B. longirostris* (mm), from Masundire (1991); (e) the relative abundance of *L. miodon*, expressed as catch per unit effort (t boat-$night^{-1}$), from Machena *et al.* (1987). The lake was isothermal from mid-June to the end of August, according to data in Magadza *et al.* (1987)

The collapse of the population in October as well as their continuing decrease in size, taking place at a time when the sardine stock was also decreasing, emphasises the importance of nutrients and food availability to plankton populations in the lake.

Limnothrissa in Lake Kariba have a short life cycle (virtually none survive for one year) and correspondingly high mortality rates (Marshall 1993a). The seasonal cycle of the zooplankton may be one of the primary causes of this situation. Cochrane (1978, 1984) showed that the condition of the fish deteriorated after the lake restratified and plankton numbers abundance decreased, i.e. from August onwards. During this period, the fish lost most of their reserves of body fat and Cochrane (1984) noted that dead fish, in very poor condition, could be found at this time of the year. He concluded that they had died of starvation.

THE LOCAL EFFECT OF THE RIVERS

In addition to determining the general level of nutrients in the lake, the rivers also influence zooplankton on a local scale and, as a rule, it is more abundant in shallow water and river mouths (see Table 4.4, also Mitchell 1975, Mills 1977). This is a consequence of the greater fertility of these areas, which is confirmed by data from the Mwenda estuary. Concentrations of nitrate and phosphate were highest at the point where the river entered the lake, decreased along the axis of the estuary and were lowest in the open lake (Figure 4.5). The density of plankton followed this trend closely.

The inflowing rivers produce some large-scale differences as well. The western Mlibizi basin (Basin 1) of the lake is greatly influenced by the Zambezi River and is riverine in character. It is relatively turbid compared to the other basins (Begg 1976, Masundire 1989b) and richer in nutrients. This is confirmed by the very much higher densities of both phytoplankton and zooplankton in this basin (Figure 4.6). The range of values was also much wider which indicates that it varies considerably which is a reflection of its riverine characteristics. The other basins are more lacustrine and do not vary to the same extent.

The rivers flowing into the eastern Sanyati basin (Basin 5) also have a pronounced effect on the distribution of the zooplankton (Marshall 1980, Masundire 1994). The Sanyati River is the largest that enters the basin but it has relatively little effect on the zooplankton. This is because the water in the Sanyati Gorge is very deep (up to 80 m at its mouth) and the incoming water flows well below the surface into the main body of the basin (Begg 1970). By contrast, the Nyaodza and Gache-Gache Rivers flow into a relatively shallow area and have a much greater effect. Thus, the density of zooplankton was highest at the mouth of these rivers, extending out into the lake (Figure 4.7). The density decreased in the open lake to the west and to the north and south. The lowest density was recorded in a shallow area east of the Sanyati which is evidently unaffected by that river or by any others.

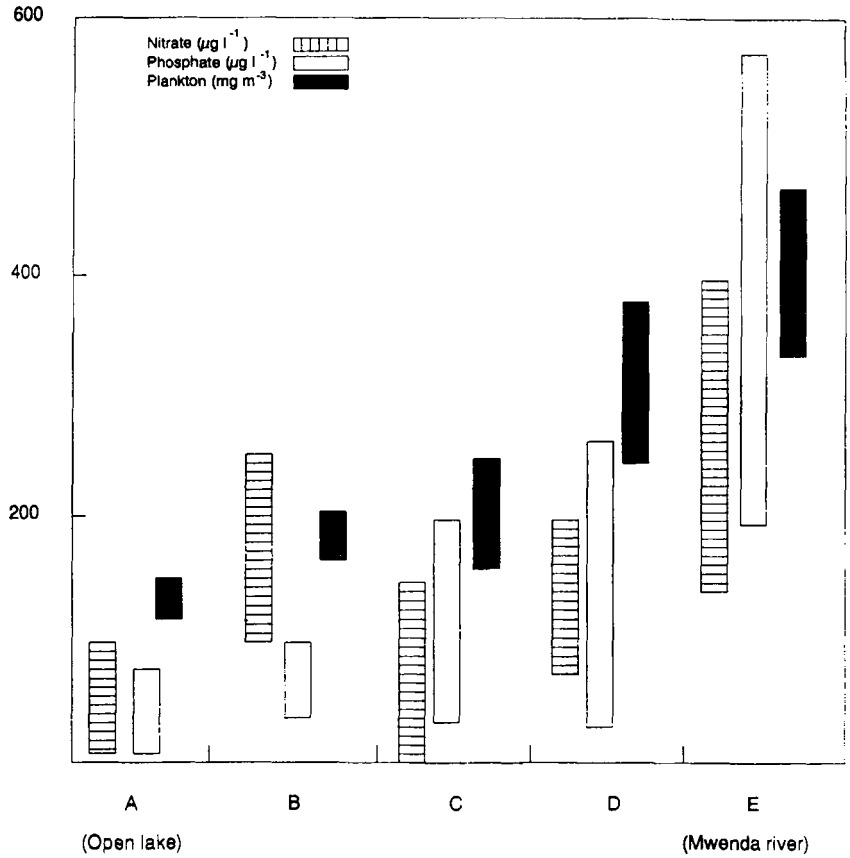

Figure 4.5 The relationship between plankton abundance and chemical nutrients in the Mwenda estuary, 1967–68. The bars show the range of values for nitrate (μg l^{-1}), phosphate (μg l^{-1}) and plankton (mg m^{-3}) at five stations from the open lake (station A) along the axis of the Mwenda estuary to the point where the river flows into the lake (station E). Redrawn from data in Bowmaker (1973)

DAILY MOVEMENTS

Daily vertical migrations are a characteristic feature of zooplankton and have been studied extensively because of their importance as a means of predator avoidance, amongst other things (see, for instance, Gliwicz 1986, Dumont and Meester 1990). This aspect of plankton ecology has not, however, been studied in much detail in Lake Kariba. It is particularly unfortunate that nothing was done before the *Limnothrissa* introduction as the behaviour of the zooplankton may have been different then (Dumont and Meester 1990).

The first studies were carried out as part of an investigation into the ecology of *Chaoborus* in 1969 (Mitchell 1975). The sampling stations were located in relatively shallow water (7 m) in the Mwenda estuary. There was no clear evidence of vertical migration although *Chaoborus* moved from the benthos to the

plankton in the early evening. The crustacea were distributed throughout the water column but there was no pattern of migration or changes of abundance in any species except *Diaphanosoma* which was most abundant from about 20.00 to 04.00 hours.

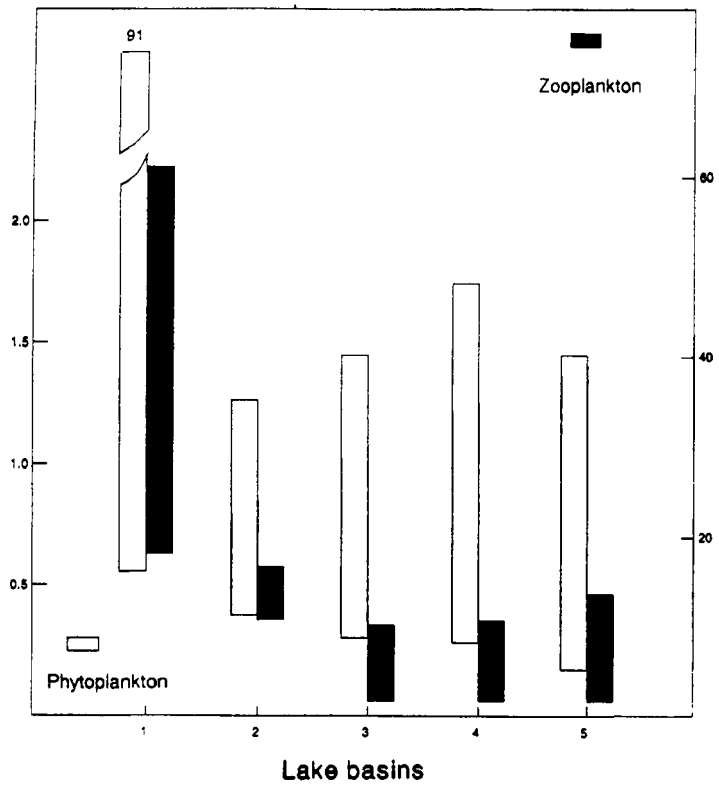

Figure 4.6 The density of plankton in the five basins of Lake Kariba. The open bars show the range of values for phytoplankton (ml l^{-1} Cronberg, 1989) while the solid bars are those for zooplankton (no l^{-1} Masundire, 1989b)

The only major investigation of vertical migration in deep water was carried out in the Sanyati basin in 1972–73 (Begg 1976). The movements of *Bosmina* were difficult to distinguish although there was some evidence of migration. The movements of adult *Mesocyclops* were much more distinct and a vertical migration could be discerned in the samples collected in August and November 1972, and February 1973 and May 1973 (Figure 4.8). There was no discernible vertical migration of nauplius larvae or most of the rotifer species. A possible exception was seen in the movements of *Monostyla quadridentatus* which was present only in February 1973. It was collected at all depths from the surface to 60 m during the daylight hours but was almost completely absent during the night. Begg considered this to be an example of irregular occurrence and not vertical migration.

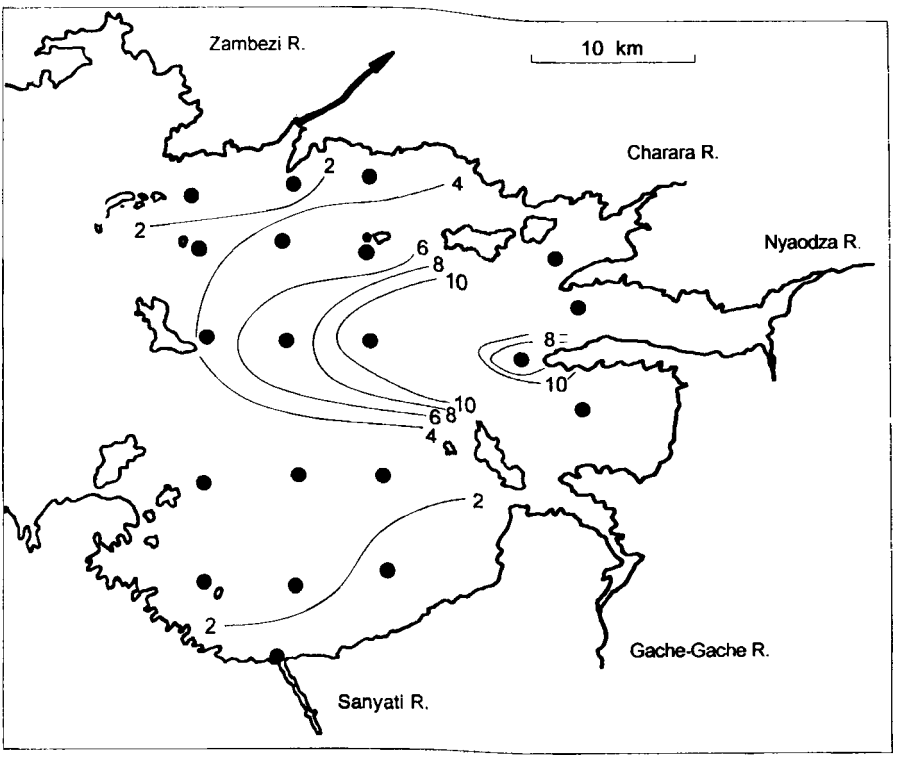

Figure 4.7 The mean density of *Bosmina longirostris* (no l^{-1}) in the Sanyati Basin, based on 6 sets of samples collected in 1986–87, showing the apparent influence of the Nyaodza and Gache-Gache Rivers. The points are the 20 sampling stations; the figure has been constructed from data in Masundire (1994)

The vertical migration of zooplankton in Lake Kariba is further limited by the thermocline and many species were restricted to the upper 30 m or so. This was especially clear in May 1973 when the lake was strongly stratified and anaerobic from 30 m down. Hydrogen sulphide was present at that depth and nothing was recorded below it.

Finally, Begg showed that *Limnothrissa* also migrated from deeper waters during the day to reach the surface by 18.00 hours, returning to deeper waters at dawn from about 06.00 hours onwards. Like the zooplankton, they were unable to go below 30 m in May 1973 because of the lack of oxygen at that depth. It was not clear if the fish were actively following the zooplankton although these movements enabled them to take advantage of the areas of greatest plankton abundance. He further suggested that the presence of the sardines may have affected the movements of *Bosmina* but did not indicate how they had done so or what these effects might have been.

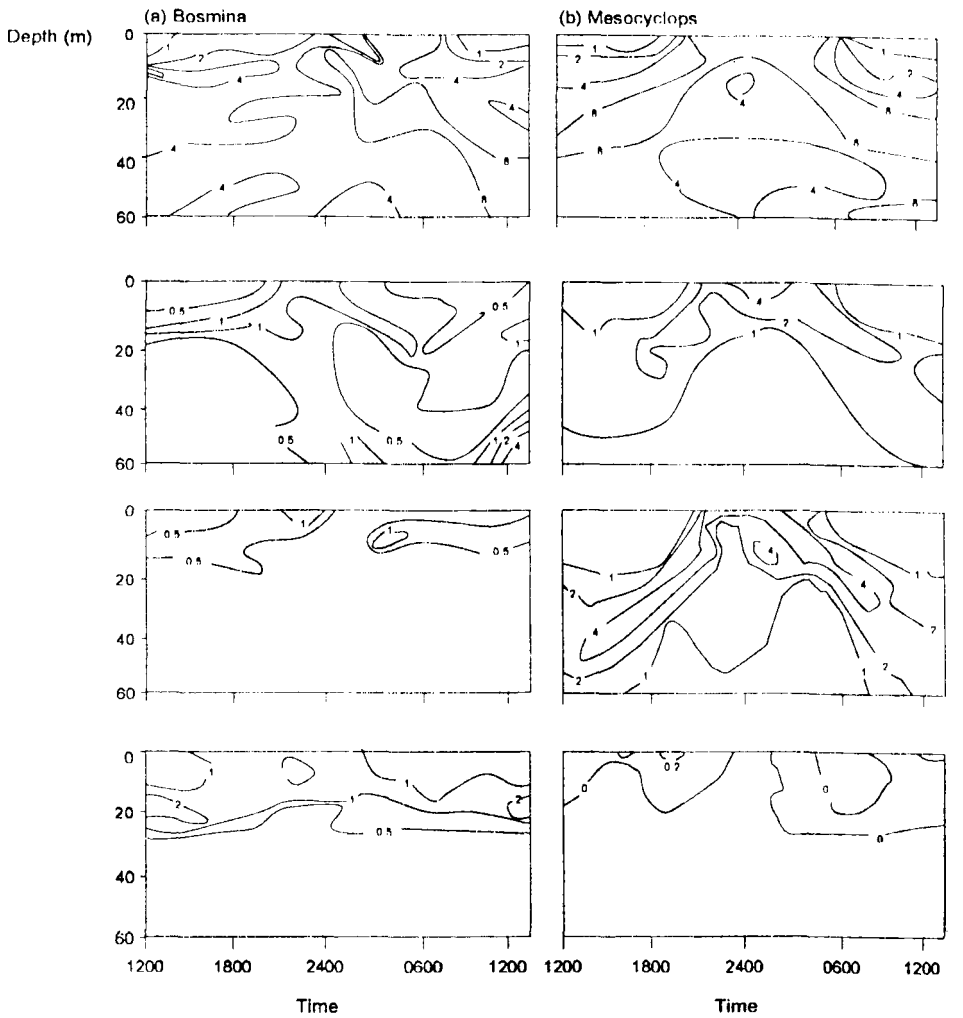

Figure 4.8 The vertical migrations over time of (a) *Bosmina* and (b) *Mesocyclops* over 24-hour periods in Lake Kariba in 1972–73. From the top to the bottom, the dates are: 14 August 1972, 21 November 1972, 6 February 1973 and 22 May 1973. Redrawn from Begg (1976)

POPULATION DYNAMICS AND PRODUCTION

Little is known about the population dynamics of the zooplankton in Lake Kariba, apart from some data on *Bosmina* in 1986 (Masundire 1992). The fecundity, birth and death rates of this species were highest from March to June (Figure 4.9) leading to an increase in the population, which reached a peak in August although these rates began to fall while the population was growing.

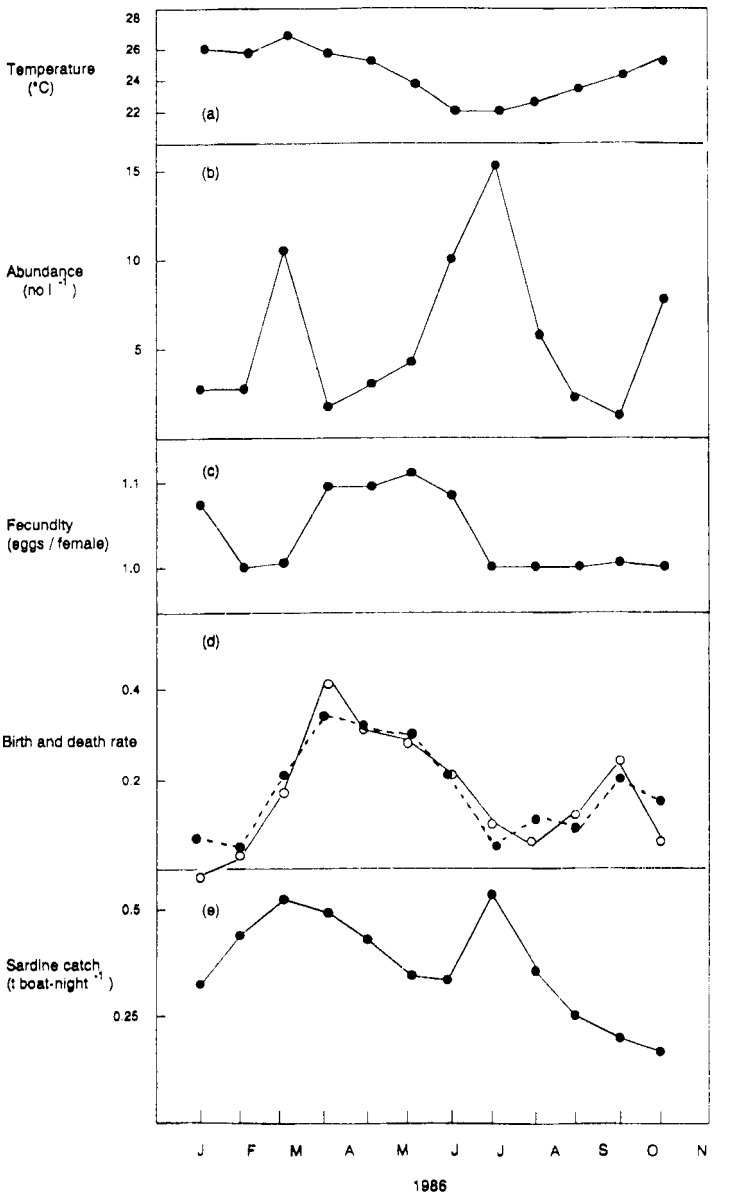

Figure 4.9 Seasonal variations in some population parameters of *Bosmina longirostris*: (a) surface temperature (°C); (b) population density (no l^{-1}); (c) fecundity (eggs per female); (d) instantaneous rates of birth (solid points, broken line) and death (open points, solid line), (e) the relative abundance of *L. miodon*, expressed as catch per unit effort (t boat-night^{-1}). All the data are from Masundire (1992) and represent mean values for station 7, except for (e) which comes from Machena *et al.* (1987)

The death rate exceeded the birth rate in March, when the population fell sharply, and again in August, October and November, a time of decreasing abundance. The birth rate was much higher in December and the numbers of *Bosmina* rose accordingly.

The data in Figure 4.9 are means from one deep water station (7) but data from a shallow station (17) are also given in Masundire (1992). The stations differ to some extent, reflecting the expected degree of variation, but the general trends are very similar.

Masundire (1992) noted that the population of *Bosmina* increased when the temperature of the water was decreasing and suggested that this variable may be an important influence on its abundance. This is questionable since the variation is very small (about 4°C) and, even at its coolest (22°C), Lake Kariba is warm. The influence of temperature is very indirect in that it controles the thermal cycle of the lake which determines when nutrients become available.

Limnothrissa is another possible influence on the population dynamics of *Bosmina*. This influence is suggested by the fact that fecundity and the birth and death rates of *Bosmina* increase at a time when the abundance of the sardine is apparently declining. This suggests that these rates may be density-dependant as they increased after the population had collapsed and may be relatively independent of predation.

The biomass of zooplankton in Lake Kariba is very low, having declined dramatically through predation by *Limnothrissa*. It seems to be much lower than that of either the phytoplankton or the sardines (Table 4.6) even allowing for uncertainties in converting estimates of wet weight to dry weight. The zooplankton biomass would be slightly greater if the rotifers had been included, but the general picture is unlikely to change.

Table 4.6 The biomass (mg m^{-3}) of the main components of the pelagic food chain in Lake Kariba, w.w = wet weight, d.w. = dry weight. Data from Ramberg (1987), Masundire (1994) and Marshall (1988b)

Species, period	*w.w.*	*d.w.*[a]
Phytoplankton, 1982–1984	310.00	77.50
Zooplankton, 1985–87[b]	157.50	15.75
Sardines, 1981–83	196.00	19.60

Note: (a) The zooplankton biomass was given as dry weight in the original source, whilst that of phytoplankton and sardines was given as wet weight. The dry weight values given in this table were computed as 25% of the wet weights.
(b) crustaceans only.

How then does a small zooplankton population support a much larger one of sardines? This is possible if the production/biomass (P/B) ratios of the zooplankton are much higher than that of the sardines. Little is known about production in the zooplankton of Lake Kariba, but an estimate can be obtained from Masundire's (1992) work on *Bosmina*. The mean rate of change of the

biomass, an approximate measure of production, was 0.65 mg m^{-3} d^{-1} (dry weight) which amounts to 237 mg m^{-3} yr^{-1} (data from station 7, located in deep water). The mean biomass of *Bosmina* in the Sanyati basin in 1986 was about 10.37 mg m^{-3} (computed from Masundire 1994) giving a P/B ratio of 22.85. In their study of trophic relationships in the lake, Machena *et al.* (1993) used a P/B ratio of 36.5 for the zooplankton community but it is not clear if this estimate includes rotifers as well as crustacea. These values are similar to those obtained elsewhere for zooplankton (Waters 1977; papers in Christensen and Pauly 1993) and are probably a reasonable representation of the zooplankton turnover rates.

Some uncertainties surround the P/B ratio of the sardine stock owing to difficulties in determining their growth and mortality rates. Various estimates, ranging from 5 to 13, have been given and the true value probably lies somewhere in between (Anon. 1992, Marshall 1993b, 1995). The P/B ratio of *Limnothrissa* is much greater than that of any other fish species in Lake Kariba but is much less than that of its prey, the zooplankton. This difference that enables the relatively small zooplankton population to support a much larger one of sardines in the face of a heavy predation.

CONCLUSION

The ecology of the zooplankton is now well known compared to that of the other communities, like the phytoplankton, in the lake. Several studies over many years make it possible to determine the impact of *Limnothrissa* and the effect of food availability on the population, its abundance and distribution.

It is important to note, nonetheless, that most of these conclusions are largely inferential. They are based on data collected by various authors over a long period of time, supplemented by a general knowledge of the behaviour of lakes rather than quantitative data. There remains an urgent need for an integrated study of the processes that influence the pelagic ecosystem. It is especially necessary to quantify energy flow between the communities and this requires an investigation which is based on simultaneous sampling at all levels.

SUMMARY

The zooplankton of Lake Kariba has attracted attention from a number of workers in the years since the lake was created. Their work is briefly reviewed in this paper. It considers firstly the species composition in the lake and then describes the changes brought about by the introduction and development of the sardine (*Limnothrissa miodon*) population. A discussion of the seasonal and diurnal cycles is followed by a consideration of the importance of the inflowing rivers. A central theme of this review is the relationship between the zooplankton and its major predator, *Limnothrissa miodon*.

ADVANCES IN THE ECOLOGY OF LAKE KARIBA

This book assembles contributions of several authors engaged in the SAREC/UZ Project on the Ecology of Lake Kariba. Various problems, regarded as particularly important, are dealt with, for instance:

- The evolution of the lake in time;
- The function of the pelagic ecosystem with focus on *Limnothrissa miodon* and the reason of variations of yields;
- The relations between the primary production and the fish production in the littoral area;
- The possible impact the large water level fluctuations on the nutrient flow and production on the grass land and in the littoral region;
- The utilisation of the mussel resource;
- The competition between fishermen, fish-eating birds and crocodiles.

This is an essential reading for students, academics and environment managers interested in tropical aquatic ecology in Zimbabwe and in the rest of the world.

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